PB84-226984

Analysis of Persistence in Model Ecosystems: Deterministic and Stochastic Food Web Models

Georgia Univ., Athens. Dept. of Mathematics

Prepared for

Environmental Research Lab., Athens, GA

Aug 84

U.S. Department of Commerce
National Technical Information Service
NTIS

PB84-226984

EPA-600/3-84-081
August 1984

ANALYSIS OF PERSISTENCE IN MODEL ECOSYSTEMS: DETERMINISTIC AND STOCHASTIC FOOD WEB MODELS

by

Thomas C. Gard
Department of Mathematics
University of Georgia
Athens, Georgia 30602

Cooperative Agreement CR807830

Project Officer

Harvey W. Holm
Environmental Systems Branch
Environmental Research Laboratory
Athens, Georgia 30613

REPRODUCED BY
NATIONAL TECHNICAL
INFORMATION SERVICE
U.S. DEPARTMENT OF COMMERCE
SPRINGFIELD, VA. 22161

ENVIRONMENTAL RESEARCH LABORATORY
OFFICE OF RESEARCH AND DEVELOPMENT
U.S. ENVIRONMENTAL PROTECTION AGENCY
ATHENS, GEORGIA 30613

TECHNICAL REPORT DATA
(Please read Instructions on the reverse before completing)

1. REPORT NO.	2.	3. RECIPIENT'S ACCESSION NO.
EPA-600/3-84-081		PB84 226984

4. TITLE AND SUBTITLE	5. REPORT DATE
Analysis of Persistence in Model Ecosystems: Deterministic and Stochastic Food Web Models	August 1984
	6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S)	8. PERFORMING ORGANIZATION REPORT NO.
Thomas C. Gard	
9. PERFORMING ORGANIZATION NAME AND ADDRESS	10. PROGRAM ELEMENT NO.
Department of Mathematics University of Georgia Athens, Georgia 30602	CCUL1A
	11. CONTRACT/GRANT NO.
	CR807830
12. SPONSORING AGENCY NAME AND ADDRESS	13. TYPE OF REPORT AND PERIOD COVERED
U.S. Environmental Protection Agency--Athens GA Office of Research and Development Environmental Research Laboratory Athens, Georgia 30613	Final, 5/81-5/84
	14. SPONSORING AGENCY CODE
	EPA/600/01

15. SUPPLEMENTARY NOTES

16. ABSTRACT

Mathematical models aid in understanding environmental systems and in developing testable hypotheses relevant to the fate and ecological effects of toxic substances in such systems. Within the framework of microcosm or laboratory ecosystem modeling, some differential equation models, in particular, become tractable to mathematical analysis when the focus is on the problem of persistence. In this report a microcosm-related, nutrient-producer-grazer, chemostat-chain model and general food web models are analyzed for persistence. The results, which take the form of inequalities involving model parameters, specify sufficient conditions for continued presence of the model components throughout indefinite time intervals. These results can serve as a basis for preliminary evaluations of model performance.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

18. DISTRIBUTION STATEMENT	19. SECURITY CLASS *(This Report)*	21. NO. OF PAGES
RELEASE TO PUBLIC	UNCLASSIFIED	15
	20. SECURITY CLASS *(This page)*	22. PRICE
	UNCLASSIFIED	

EPA Form 2220-1 (9-73)

DISCLAIMER

Although the research described in this report has been funded in part by the United States Environmental Protection Agency through cooperative agreement CR807830 to the University of Georgia, it has not been subjected to the Agency's required peer and policy review and therefore does not necessarily reflect the views of the Agency.

FOREWORD

Environmental protection efforts are increasingly directed towards preventing adverse health and ecological effects associated with specific compounds of natural or human origin. As part of this Laboratory's research on the occurrence, movement, transformation, impact, and control of environmental contaminants, the Environmental Systems Branch studies complexes of environmental processes that control the transport, transformation, degradation, and impact of pollutants and other materials in soil and water and assesses environmental factors that affect water quality.

Mathematical models are increasingly being used by environmental scientists as tools for understanding the behavior of pollutants in water. Some of these models take the form of differential equations that describe the growth-decay rate of components of the aquatic system being modeled. This report presents a technique for the mathematical analysis of persistence as a guage of model performance.

William T. Donaldson
Acting Director
Environmental Research Laboratory
Athens, Georgia

ABSTRACT

Mathematical models aid in understanding environmental systems and in developing testable hypotheses relevant to the fate and ecological effects of toxic substances in such systems. Within the framework of microcosm or laboratory ecosystem modelling, some differential equation models, in particular, become tractable to mathematical analysis when the focus is on the problem of persistence. In this report a microcosm-related nutrient-producer-grazer chemostat-chain, and general food web models are analyzed for persistence. The results, which take the form of inequalities involving model parameters, specify sufficient conditions for continued presence of the model components throughout indefinite time intervals. These results can serve as a basis for preliminary evaluations of model performance.

This report was submitted in fulfillment of Cooperative Agreement CR807830 by the University of Georgia Research Foundation, Inc. under the sponsorship of the U.S. Environmental Protection Agency. This report covers the period May 20, 1981 to May 19, 1984. The work was completed as of May 1, 1984. This report represents the opinion of the author. It carries no official endorsement by the University of Georgia.

SECTION 1

INTRODUCTION

Certain mathematical models of environmental systems take the form of differential equations, with each equation describing the growth-decay rate of a substance or an organism constituting a component of the environmental system modelled. In general the differential equations are nonlinear and exact solutions in terms of elementary functions are impossible to obtain. In this case, the mathematics appropriate to analyzing such models involves approximation techniques, of which there are two fundamental types. One method is to directly approximate the solutions; algorithms for generating numerical solutions by computer are used to implement this method. This approach is effective if parameter values in the model are reasonably well-known and if interest is focused on solutions corresponding to limited sets of initial values for the model components. The second method essentially deals with approximating the differential equations and obtaining information about the solutions by comparison with solutions of the (hopefully) simpler approximating system. The technique here consists of constructing auxiliary functions and differential inequalities and has an algebraic character. The results are qualitative rather than quantitive and, although less specific, nevertheless are valid over wider ranges of parameter and initial values. The work reported on here exemplifies this second method of analysis.

Persistence in mathematical models of ecosystems is the analogue for survival of organisms and continued presence of substances in the systems modelled and hence is a very relevant aspect of such models in terms of the mission of the Environmental Protection Agency. In the context of differential equation models, the problem of determining persistence can be approached by the qualitative techniques of analysis described above. The results are formulated as ranges of model parameter values for which persistence holds.

SECTION 2

DESCRIPTION OF RESEARCH

GENERAL SETTING

The research reported on here deals with the mathematical analysis of models of ecological subsystems.. The mathematical models take the form of a system of ordinary differential equations

$$x_i' = f_i(x_1,\ldots,x_n) \qquad i=1,\ldots,n \qquad (1)$$

$$\left[' = \frac{d}{dt}\right]$$

or an analogous system of random differential equations

$$x_i' = f_i(x_1,\ldots,x_n) + \sum_{j=1}^{m} g_{ij}(x_1,\ldots,x_n)N_j \qquad i=1,\ldots,n. \qquad (2)$$

In (1) and (2) the state variable $x_i(t)$ represents the ith component substance or organism density at time t for the ecological subsystem modelled. The function f_i in (1) gives the net rate of growth or decay of the ith component in terms of all state variables at time t. In (2) the ensemble $\{N_j(t),j=1,\ldots,n\}$ denotes a collection of independent unit intensity white noise stochastic processes; thus the terms $g_{ij}\,N_j$ represent independent random environmental fluctuations with intensity g_{ij} about the average growth rate f_i. The mathematical ambiguity of (2) (due to the pathological nature of white noise) and certain approximation results for stochastic population models motivate the specific interpretation of (2) as the system of Ito type stochastic differential equations

$$dx_i = f_i(x_1,\ldots,x_n)dt + \sum_{j=1}^{m} g_{ij}(x_1,\ldots,x_n)dW_j \qquad i=1,\ldots n \quad (3)$$

where the $W_j(t)$, $j=1,\ldots,m$, are independent Brownian motion processes. (Formally, $W_j'(t) = N_j(t)$). Although the same notation is used, it is important to note the distinction between solutions of (1) and (3). In (1), for a fixed value of t, $x_i(t)$ denotes a number - the determined population density of the ith component at time t. On the other hand, in (3) for fixed t, $x_i(t) = x_i(t,\omega)$ is a random variable (ω, the probability space variable is usually suppressed) with a distribution indicating the relative likelihood of the possible sample population density values. In each case, of interest are solutions $x(t) = (x_1(t),\ldots,x_n(t))$ which remain in the feasible region

$$R_+^n = \{(x_1,\ldots,x_n): x_i \geq 0, \text{ all } i\}$$

and in particular solutions with initial values $x(0)$ in the interior of the feasible region

$$R_+^{n,o} = \{(x_1,\ldots,x_n): x_i > 0, \text{ all } i\}.$$

Indeed, under mild assumptions on the functions f_i and g_{ij} consistent with applications, for any initial value x^o in $R_+^{n,o}$ there exists a unique solution $x(t)$ satisfying $x(0) = x^o$ which remains in $R_+^{n,o}$ for t in some interval $[0,T)$. Persistence for the ith component $x_i(t)$ of a solution of (1) means

$$\lim_{t\to T} x_i(t) \neq 0. \tag{4}$$

For models of type (3), the appropriate notion is stochastic boundedness persistence: for each $\varepsilon > 0$, there is a positive constant $L(\varepsilon)$ such that

$$\text{Probability}[x_i(t) \geq L(\varepsilon), \text{ all } t \text{ in } [0,T)] \geq 1 - \varepsilon. \tag{5}$$

Stochastic boundedness persistence was proposed by Chesson (1978,1982) who pointed out its biological interpretation: trends to ever lower population densities are impossible and the average frequency of fluctuations to low density does not increase with time. The research carried out under this grant focused specifically on persistence for top predators in food web models of type (1) and (3). The work extends results previously reported (Gard, 1982).

NPZ MICROCOSM MODEL

Microcosms or laboratory ecosystems are important tools in environmental systems analysis, and related mathematical models have been proposed to investigate the structure complexities in such ecosystems (Lassiter, 1978). A mathematical analysis for these models was carried out previously (Gard, 1981), but for the most complicated of these models which included a nutrient(N)-producer(P)-grazer(Z) chemostat-chain, a sufficient condition for persistence could only be conjectured. The model can be written:

$$\begin{aligned} N' &= a(t) - N\left(d_N + b_P \frac{P}{c_P + N}\right) \\ P' &= P\left(b_P \frac{N}{c_P + N} - d_P - \frac{b_Z}{k} \frac{Z}{c_P + P}\right) \\ Z' &= Z\left(b_Z \frac{P}{c_Z + P} - d_Z\right) \end{aligned} \tag{6}$$

The parameters

maximum growth rates: b_P, b_Z

net death and washout rates: d_N, d_P, d_Z

half saturation constants: c_P, c_Z

yield coefficient: k

are assumed to be positive constants with yield coefficient less than one, and without loss of generality, d_N can be taken as one; the function $a(t)$ represents time-varying external nutrient input to the NPZ system, and in the results that follow it is assumed that there are postive constants a_0 and a_1 such that

$$a_0 \leq a(t) \leq a_1, \text{ all } t \geq 0$$

Let $d_m = \min\{1, d_P, d_Z\}$, $d_M = \max\{1, d_P, d_Z\}$

$$A_0 = a_0/d_M, \quad A_1 = a_1/d_m.$$

The main results obtained (Gard, 1983) are: every solution $x(t) = (N(t), P(t), Z(t))$ of (6) with initial value $x(0) \in R^3_{+,o}$ satisfies

$$x(t) \to \{(N,P,Z): A_0 \leq N + P + \frac{1}{k} Z \leq A_1\} \text{ as } t \to \infty; \qquad (7)$$

and persistence holds for Z if

$$a_0 > \frac{d_P}{b_P - d_P}\left[c_P + \frac{(A_1 + c_Z)\, b_P^2\, d_Z}{(b_P - d_P) b_Z}\right]. \qquad (8)$$

It must be noted that (8) is fairly restrictive; the presence of A_1 on the right side requires b_Z to exceed some minimum value just for consistency of (8). For the special case of constant nutrient input $a(t) = a_0$, all t, the less restrictive persistence condition

$$a_0 > \frac{c_P\, d_P}{b_P - d_P} + d_P\left[\frac{c_Z\, d_Z}{b_Z - d_Z}\right] \qquad (9)$$

was obtained.

The main technique used to establish (8) and (9) involved the construction of a two-parameter family $\rho(N,P,Z;r,s)$ of auxiliary functions, each with the property that ρ tends to zero with Z; also for each function ρ, the derivative of ρ

$$\dot{\rho} = \frac{d\rho(N(t),P(t),Z(t);r,s)}{dt}$$

along solution curves can be expressed in terms of the right side of (6).

Conditions (8) and (9) each permit a choice of the constants r and s so that the corresponding ρ satisfies

$$\dot{\rho} > 0$$

at least for Z sufficiently close to zero and $X = (N,P,Z)$ sufficiently near the set in (7). Thus ρ cannot tend to zero, and so neither can Z.

FOOD WEB MODELS

The ability to predict ecological effects of introducing a toxic substance into food web subsystems would complement toxic substance fate studies carried out by the U.S. Environmental Protection Agency. A basic ecological effect for food webs is trophic structure preservation which corresponds to the food web model condition: for each initial density configuration with all components positive, at least some component corresponding to a top predator survives indefinitely. The PZ subsystem of (6), discussed in the previous section exemplifies the basic food web structure, namely the prey-predator relationship; conditions (8) and (9) establish minimum levels for the nutrient resource input which will assure preservation of the structure in this case. In this section comparable persistence results are given for a general deterministic food web model and for an analogous stochastic food web model in which random environmental fluctuations are explicitly taken into account (Gard, 1984 a,b).

The deterministic food web model takes the form:

$$x_i' = x_i\left(a_i - \sum_{j=1}^{k} b_{ij}x_j - \sum_{j=1}^{m} c_{ij}y_j\right) \qquad i=1,\ldots,k$$

$$y_i' = y_i\left(-d_i + \sum_{j=1}^{k} e_{ij}x_j - \sum_{j=1}^{p} f_{ij}z_j\right) \qquad i=1,\ldots,m \qquad (10)$$

$$z_i' = z_i\left(-g_i + \sum_{j=1}^{m} h_{ij}y_j\right) \qquad i=1,\ldots,p$$

in the feasible region R_+^n, $n = k + m + p$, where $x_i = x_i(t)$, $y_i = y_i(t)$, $z_i = z_i(t)$ represent the densities of ith prey, intermediate predator, and top predator, respectively; the coefficients $a_i, b_{ij}, c_{ij}, d_i, e_{ij}, f_{ij}, g_i$, and h_{ij} represent growth and interaction rates which are taken to be nonnegative bounded functions of t, $x = \{x_i\}$, $y = \{y_i\}$, and $z = \{z_i\}$; for example, for the coefficients $a_i = a_i(t,x,y,z)$, it is assumed that there are nonnegative constants $\underline{a}_i$ and $\overline{a}_i$ such that, for all t,x,y,z,

$$\underline{a}_i \leq a_i \leq \overline{a}_i.$$

Similar notation denotes the bounds on the other coefficients.

Solutions of (10) with initial values (x^o,y^o,z^o) in $R_+^{n,o}$ are bounded; furthermore top predator persistence ((4) is satisfied for at least some z_i) for each such solution is assumed if

$$\mu = \sum_{i=1}^{k} \underline{a}_i - \sum_{i=1}^{m} \bar{d}_i r_i - \sum_{i=1}^{p} \bar{g}_i s_i > 0 \qquad (11)$$

for a solution $\{r_i\}$ and $\{s_i\}$ of the auxiliary linear programming problem

$$\text{minimize} \quad \sum_{i=1}^{m} \bar{d}_i r_i + \sum_{i=1}^{p} \bar{g}_i s_i \quad \text{subject to}$$

$$r_i \geq 0, \; s_i \geq 0$$

$$\sum_{j=1}^{m} \underline{e}_{ji} r_j - \sum_{j=1}^{k} \bar{b}_{ji} \geq 0, \qquad i=1,\ldots,k \qquad (12)$$

$$\sum_{j=1}^{p} \underline{h}_{ji} s_j - \sum_{j=1}^{k} \bar{c}_{ji} \geq 0, \qquad i=1,\ldots,m.$$

The parameter μ represents a minimum weighted net growth rate for the food web; the weights (r_i and s_i) are restricted by bounds on the interaction rates. Working with bounds on the coefficients rather than assuming constant coefficients is one way to deal with the important question of parameter uncertainty. Another approach to this problem, which explicitly involves random fluctuations of the parameters, proceeds from the stochastic analogue of (10)

$$dx_i = x_i[(a_i - \sum_{j=1}^{k} b_{ij}x_j - \sum_{j=1}^{m} c_{ij}y_j)dt + \sum_{j=1}^{q} \sqrt{\sigma_{ij}^{(x)}}\, dW_j] \qquad i=1,\ldots,k$$

$$dy_i = y_i[(-d_i + \sum_{j=1}^{k} e_{ij}x_j - \sum_{j=1}^{p} f_{ij}z_j)dt + \sum_{j=1}^{q} \sqrt{\sigma_{ij}^{(y)}}\, dW_j] \qquad i=1,\ldots,m \qquad (13)$$

$$dz_i = z_i[(-g_i + \sum_{j=1}^{m} h_{ij}y_j)dt + \sum_{j=1}^{q} \sqrt{\sigma_{ij}^{(z)}}\, dW_j] \qquad i=1,\ldots,p.$$

Now consider the set

$$R = \{(x,y,z) \in R_+^n : x_i \le \gamma_i^{(x)},\ y_i \le \gamma_i^{(y)},\ z_i \le \gamma_i^{(z)},\ \text{all } i\}$$

where the $\gamma_i^{(x)}$, $\gamma_i^{(y)}$, and $\gamma_i^{(z)}$ are arbitrarily chosen positive constants. Assume the bound assumptions and notation on the coefficients of (13) including the noise intensities σ_{ij} in R as in the deterministic case. The following result requires that the lower bound for some $\sigma_{ij}^{(z)}$ each i, be positive. Suppose that

$$\mu > \frac{1}{2} \sum_{j=1}^{q} \left(\sum_{i=1}^{k} \bar{\sigma}_{ij}^{(x)} + \sum_{i=1}^{m} r_i \bar{\sigma}_{ij}^{(y)} + \sum_{i=1}^{p} s_i \bar{\sigma}_{ij}^{(z)} \right) \qquad (14)$$

where μ is given in (11) and r_i and s_i solve the linear programming problem

$$\text{minimize} \sum_{i=1}^{m} r_i \left(\bar{d}_i + \frac{1}{2} \sum_{j=1}^{q} \bar{\sigma}_{ij}^{(y)} \right) + \sum_{i=1}^{p} s_i \left(\bar{g}_i + \frac{1}{2} \sum_{j=1}^{q} \bar{\sigma}_{ij}^{(z)} \right) \qquad (15)$$

subject to the same constraints as in (12). Then, for any solution $(x(t),y(t),x(t))$ of (13) with initial value (x^o,y^o,z^o) in the interior of R, stochastic boundedness persistence (5) holds with $T = T_R$, the first exit time of the solution from R, for at least some z_i.

Note that in the deterministic case, μ positive sustains the trophic structure, while in the stochastic case, the analogous condition requires μ to exceed a weighted sum of the fluctuation intensities. The results in the section readily extend to food web models with more than three trophic levels, and those that exhibit arbitrary degrees of omnivory and competition for space among same trophic level predators. Similarly to the NPZ model analysis, the principal mathematical technique used to establish the results involved the construction of a Liapunov like auxiliary function.

UTILIZATION OF RESULTS BY EPA MODELERS

Basically the results obtained here indicate that some top predator (which one may depend on initial data) in the food web survives indefinitely if certain conditions on model parameter bounds are met. This means that the trophic structure, rather than any specific species ensemble, is preserved in the food web if the conditions hold. For the EPA modeler, then, these results provide a check that a proposed model mimics an important ecological effect, at least.

To apply the results one first needs to determine bounds for the various coefficients involved in the particular model of interest; hopefully these can be estimated from experimental data and intuition about the specific system modeled. Then using the parameter bounds as input one solves the linear programming problem (12), for the deterministic case, or (15), for the stochastic case, and thus determines viable choices for the auxiliary constants r_i and s_i. Substitution of the r_i and s_i into the expressions in (11) or (14) allows one to check whether these inequalities are valid, i.e., whether some top predator persists for any feasible ensemble of initial population density levels for the species in the web.

SECTION 3

SUMMARY

The mathematical analysis focusing on persistence in differential equation models of current and future potential interest to the U.S. Environmental Protection Agency results in criteria taking the form of inequalities involving model parameters. For the NPZ microcosm-related model, the main result is expressed in terms of a threshold value for the nutrient input rate. In the case of deterministic food web models, positivity of minimum weighted net growth rates constitute the persistence conditions. For stochastic food web models, these net growth rates must exceed corresponding weighted sums of the random fluctuation intensities. Generally, the nutrient input level, or the total intrinsic growth rate of the food sources being sufficiently large guarantees persistence. The methods used consist of approximating the differential equations; in particular, the auxiliary function-comparison principle techniques are the main tools employed from the qualitative theory of ordinary and stochastic differential equations. The extension of the results previously reported to the case of general food web models demonstrates the robust nature of this approach to the problem of ecosystem model stability.

REFERENCES

1. P. Chesson, Predator-prey theory and variability, Ann. Rev. Ecol. Syst. 9 (1978), 323-347.

2. P. Chesson, The stabilizing effect of a random environment, J. Math. Biol. 15 (1982), 1-36.

3. T.C. Gard, Persistence for ecosystem microcosm models, Ecol. Modelling 12 (1981), 221-229.

4. T.C. Gard, Persistence in model ecosystems, U.S. Environmental Protection Agency Report No. EPA - 600/3-82/030, 1982.

5. T.C. Gard, Mathematical analysis of some resource-prey-predator models: application to a NPZ microcosm model, Proc. Int. Conf. Pop. Biol, Edmonton, 1982, H.I. Freedman and C. Strobeck (eds.), Lecture Notes in Biomath., 52, Springer-Verlag, 1983, 275-282.

6. T.C. Gard, Persistence in food webs, Proc. Int. Conf. Math. Ecol., Trieste, 1982, T.G. Hallam and S.A. Levin (eds.), Lecture Notes in Biomath., 54, Springer-Verlag, 1984, 208-219.

7. T.C. Gard, Persistence in stochastic food web models, Bull. Math. Biol. 46(1984), 357-370.

8. R.R. Lassiter, Microcosms as ecosystems for testing ecological models, State-of-the-Art in Ecol. Modelling, Vol.7, Proc. 1st Int. Conf. Ecol. Modelling, Copenhagen, 1978, S.E. Jorgensen (ed.), ISEM, 1978.